Pl. LIV.

Fig. 20. Blood of a Palm Tanager showing infection with *Hæmoproteus danilewskyi*. Three full-sized parasites are present, and some early forms are seen in the photograph as dots in the erythrocytes.

Fig. 21. Blood of a Bengal Monitor showing an ordinary hæmogregarine and the one mentioned on p. 412 of text. × 450. This is probably a double infection as no intermediate stages between these parasites can be seen.

At *a* the ordinary form of hæmogregarine is seen; those erythrocytes marked *b* contain the new type of parasite, to which reference has been made in the text. This parasite stains badly, there is a very small amount of nuclear material in it when stained by any modification of the Romanowsky method or by iron-logwood, and the altered nucleus of the erythrocyte stains very densely.

Fig. 22. Drawings of the same parasites. At *a* the ordinary hæmogregarines are shown, and at *b* the other parasite, in an early stage in the drawing to the left, and in the later stage, with the cell-nucleus divided, to the right.

Pl. LV.

Fig. 23. Drawings of the new parasite.

The erythrocyte in the photograph and drawings is seen to be deformed, and eventually dehæmoglobinised (as in the cell marked *a*). At *b* is seen the tiny nodule which is generally to be found on the delicate connecting-thread between the pieces of the cell-nucleus. The cell marked *c* contains what appears to be an abortive attempt to divide the cell-nucleus equally: very few of these were found.

Fig. 24. Drawings of forms found in the lungs, showing various stages in schizogony. None of these small forms have been found in the erythrocytes. No stages were found in the other organs.

23. On the Structure of the Internal Ear and the Relations of the Basicranial Nerves in *Dicynodon*, and on the Homology of the Mammalian Auditory Ossicles. By R. Broom, M.D., D.Sc., C.M.Z.S.

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(Plate LVI.* and Text-figure 53.)

Few questions connected with vertebrate morphology have given rise to a larger amount of discussion than the homology of the mammalian auditory ossicles and the connected problem of the fate of the quadrate in mammals. Most embryologists have been struck with the resemblance of the malleus and incus to an articular and quadrate; many comparative anatomists have been impressed rather with the resemblance of the mammalian auditory chain with the auditory apparatus of the Reptilia; while palæontologists, for the most part, have hesitated to believe that the incus could be the quadrate, from the difficulty of imagining the intermediate stages, and have inclined rather to believe that the quadrate has become part of the zygomatic arch, or the meniscus, or become lost, or converted into the tympanic bone.

Until a few months ago I was of opinion that the quadrate became either the meniscus or, in those few forms where a meniscus is absent, was lost. It is unnecessary to repeat the arguments by which I have endeavoured to maintain this position; suffice it to say that I now regard the position as untenable, since the element in the Anomodonts which I have long regarded as the tympanic now proves to be unquestionably the stapes.

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* For explanation of the Plate see p. 425.

In the type skull of *Dicynodon latifrons* there is a slender rod-like bone lying in the cavity which is bounded above by the exoccipital, and usually by a dumbbell-like bone below. The stout dumbbell-like bone which stretches from the basioccipital process to the quadrate I have hitherto believed to be the tympanic, and the slender rod-like bone the stapes. New evidence now shows that whatever the slender bone may be—perhaps a displaced part of the hyoid—the supposed tympanic is undoubtedly the stapes, and what I believed to be the fenestra ovalis is the foramen for the viith nerve.

Having the imperfect occiput of a moderate sized *Dicynodon*, in which the matrix was much hardened by epidote and the bone mainly calcareous, I saw it might be possible to dissolve the bone and leave a cast of the internal ear and the basicranial nerve-passages. Though on one side much of the internal ear was found to be occupied by calcite, the result of the decalcification on the whole was so satisfactory that the structure of the ear in *Dicynodon* is now almost as well known as in recent animals, and as much is known of the cranial nerves as is ever likely to be known.

The internal ear (Pl. LVI. figs. 1–3) is unlike that of any animal hitherto described, so far as I am aware. While the semicircular canals are apparently not unlike those of recent reptiles or mammals, the vestibule is very remarkably elongated and there is no trace of a cochlea.

The vestibule has an upper, somewhat triangular portion, which lies between the upper end of the canal for the viith nerve and the upper end of that for the ixth, xth, and xith nerves. In close contact with the brain cavity there is an upward extension, with which is united the canal common to the anterior and posterior semicircular canals. On the anterior and posterior sides are irregular excrescences, which are perhaps vascular spaces filled with matrix. The broadest part of the vestibule is where the ampullæ of the anterior and posterior semicircular canals are situated. From this point the vestibule passes downwards for a distance about twice as great as the maximum width. To near the middle of this descending portion there is a steady narrowing, but beyond the middle the vestibule again expands and the fenestra ovalis is about as wide as the widest part of the vestibule. The fenestra ovalis lies near the middle of the descending basioccipital process, but looks outwards and slightly downwards. This large descending process, so conspicuous in the Anomodont skull, is formed posteriorly by the basioccipital bone, and in front it is supported by the basisphenoid, but there seems considerable reason for believing that the centre portion is partly prootic and partly opisthotic. Down the descending part of the vestibule there appears to be evidence of the suture between the two otic bones.

The semicircular canals are lost from the left side of the specimen, and though they are preserved on the right side, as they are partly filled with calcite and the bone is much epidotised, it is impossible satisfactorily to decalcify the right side. Still, sufficient has been successfully accomplished to show at least a part of each canal.

The posterior semicircular canal has a distinct ampulla, which lies very close to the canal for the ixth, xth, and xith nerves. From here it passes upwards and forwards, then inwards, and lastly downwards, doubtless uniting with the upper end of the anterior canal.

The horizontal canal, though well shown in its middle region, has neither its anterior nor posterior ends displayed. The position of the canal will be better understood from the figure than from description.

The anterior semicircular canal is badly displayed. It runs mainly upwards to unite with the descending part of the posterior canal.

The cast of the posterior portion of the cranial cavity and of the basicranial nerves is beautifully preserved.

Behind the lower end of the posterior semicircular canal is seen the cast of the large canal for the ixth, xth, and xith nerves; where it leaves the cranial cavity it is slightly extended antero-posteriorly, but where it leaves the skull it is flattened a little vertically.

The canal for the xiith nerve passes down a short distance behind the jugular foramen, and unites with it before it leaves the skull. The fact that the xiith nerve has only a single canal is interesting in view of the fact that in the Cotylosauria, as exemplified by *Pareiasaurus*, we have two foramina for the xiith nerve, and a similar condition is found in the Cynodontia and in the Marsupialia. In the Pelycosauria, as has been shown by Case, and in the Eutheria, there is, as in the Anomodontia, only a single foramen for the xiith nerve.

The canal for the viith nerve lies a little in front of the vestibule. It is long and narrow and passes downwards and slightly outwards, and ends in the small foramen seen at the bottom of the deep groove between the back part of the basisphenoid and the pterygoid.

In front of the specimen is seen the deep pituitary fossa, and below it the carotid canal. The latter begins at a small rounded foramen near the front of the posterior processes of the basisphenoid. The main part of the canal passes upwards, forwards, and slightly inwards, and unites with the canal of the opposite side just in front of the hypophysis. From the lower end of the canal is given off a smaller canal, which passes upwards and somewhat more forwards. While the large canal is pretty certainly that for the carotid artery, the smaller is possibly for the *arteria ophthalmica*. Whatever be the condition of the arteries within the cranial cavity, it must have been very unlike that of *Sphenodon* or other living reptiles, and though perhaps a little more like the condition in mammals, the resemblance could not have been very close.

The stapes has long been an element which gave rise to difficulties. So far as I am aware, the first author who gave a good figure of the bone was P. Fischer, in 1870, and he regarded the element as the pterygoid. From nearly all the British Museum skulls it has been removed during development, but it still remains and is well shown in the skull which forms the type of *Kistecephalus chelydroides*. Unfortunately, unlike most of Griesbach's work, his figure of this skull in Owen's Catalogue is rather poor, and in the description Owen says nothing about the bone in question. But in any case, as Owen mistakes a portion of the squamosal for the quadrate (his "tympanic"), though the quadrate itself is present in a fairly well-preserved condition, it is manifest that he had not a very clear idea of the structure of this part of the skull. Seeley, when studying the Anomodont skull in 1888, took the massive stapes to be a malleus, and the unquestionably homologous bone in the Cynodonts he later described as possibly a "straight cochlea." Hitherto, I have always looked upon it as the tympanic. Now we know that it is certainly the stapes, though so very unlike the stapes of any living form.

Though a considerable number of Anomodonts are known showing the stapes in position and in perfect condition, I shall describe and figure it and the related bones from the beautiful specimen which I have recently made the type of *Oudenodon kolbei* (Pl. LVI. figs. 4–6). The stapes is here a short dumbbell-shaped bone with the ends flattened and slightly oblique. Across one diagonal it measures 30 mm., across the other 23 mm. The narrowest part of the middle measures 12 mm. across. When viewed from behind the stapes is seen to be much flattened, the narrowest part of the bone measuring only 4 mm. in thickness. A considerable part of the inner end has probably been cartilaginous. The outer end is much flattened and is closely articulated to the inner side of the quadrate. There seems to be no supra- or extra-columella, or if there has been one it must have been relatively very small.

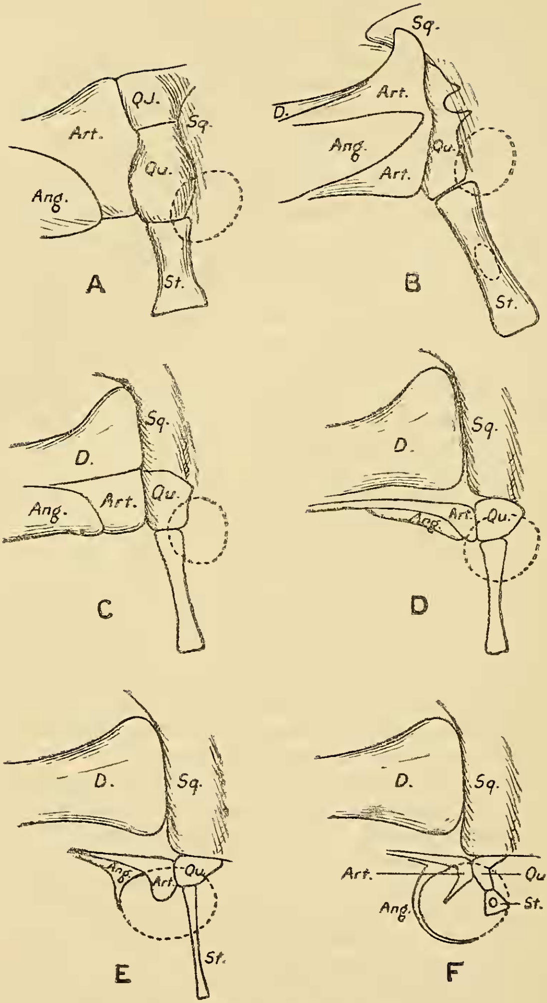
The quadrate, one would readily think, would be the most easy bone in the skull to identify. Many years ago Owen figured what he believed to be the quadrate, and nearly everyone has agreed with his determination. There is a large articulation, about as broad as long. Along its inner third there runs an antero-posterior ridge; near the middle there is an antero-posterior shallow groove; and the outer part of the articulation is a convex disc. This outer part forms the base of a bone which on passing upwards becomes a wide fan-like squamous plate, which is closely applied to the squamosal. If the whole articulation be quadrate this squamous plate must also be quadrate, as has been the view of Owen, Seeley, and myself. It would now appear that about half of the articulation is formed by the quadrato-jugal, and that the squamous plate is also thus quadrato-jugal.

The squamosal comes down behind the quadrate and quadrato-jugal almost to the articulation. A shallow but distinct groove can be traced down, partly formed by the squamosal and partly by the exoccipital. This is evidently for the external auditory canal, but how the tympanic membrane was attached or whether there was one at all, the evidence does not show. Not improbably there was a membrane attached to the exoccipital, squamosal, and to a small part of the quadrate.

Though the articular region is more perfectly known in the Anomodonts than in other Therapsida, a good deal is known about its condition in the other groups. In the Pelycosaurs the stapes is large and of a peculiar shape, the quadrate is also large and forms the whole of the articulation, and a small quadrato-jugal is present. Little is known of the condition in the Dromasauria. In the Dinocephalia the quadrate is large and forms the whole articulation, and a quadrato-jugal is apparently always present. It is known in *Delphinognathus*, *Moschops*, and *Tapinocephalus*. The stapes is probably very similar to that in the Anomodontia. In the Therocephalia the quadrate is small, but forms the whole articulation. No quadrato-jugal is known in any genus. The stapes is not well known, but appears to be large and long. In the Cynodonts a quadrato-jugal is never present and the quadrate is usually small. In some genera (e.g. *Cynognathus*) a considerable part of the articular surface for the lower jaw is formed by the squamosal, the quadrate forming only about three-fourths of the joint. The stapes in *Bauria* and *Cynognathus* is a fairly strong cylindrical rod: in *Trirachodon* it is also a long rod, but very slender. In all these genera its outer end is firmly attached to the quadrate.

As there are very strong reasons for believing that the mammals are descended from one of the mammal-like reptiles, probably a primitive Cynodont, all the information that can be obtained on the structure of the auditory apparatus is especially welcome, because of the light it may throw on the nature of the mammalian auditory ossicles. And the certain determination of the stapes seems to settle the homologies of the various elements. Had the outer end of the stapes been free and given attachment to a cartilaginous extrastapedial, the dispute might have gone on. But there is apparently no extrastapedial, and certainly the greater part of the outer end of the stapes is firmly fixed to the quadrate. The similar attachment of the stapes to the incus in mammals is striking; and though I have long advocated another view, I now feel forced to agree to the view that the incus is the reptilian quadrate, as advocated so many years ago by Reichert. The slipping out of the quadrate from the joint is not now a very serious difficulty, for in *Cynognathus* we see it already partly slipped out. Nor is there any very great difficulty in understanding how the new dentary-squamosal joint arose. In *Cynognathus*, the posterior end of the dentary nearly takes part in the joint, and there is no difficulty in realising the next stage in the evolution, where the dentary and articular together hinged on the squamosal and the quadrate. As the direct articulation of the dentary on the squamosal became more firmly established, the

Text-fig. 53.



A. Diagrammatic representation of articulation in *Dicynodon*.

B. Articulation in the Cynodont, *Cynognathus*.

C. Hypothetical diagram of the condition when the dentary articulates with the squamosal.

D. Hypothetical diagram of the condition when the articular and angular no longer support the jaw.

E. Hypothetical diagram of the condition when the articular and angular take on their auditory function.

F. Diagram representing the perfecting of the auditory function (the mammalian condition).

quadrate, articular, and angular degenerated, and might have been lost had not the attachment of the stapes to the quadrate compelled them to take on an auditory function.

The tracing of the steps by which the articular became the malleus and how the manubrium was formed is a matter of some difficulty in our ignorance of the position of the tympanic membrane, but we may assume as very probable that soon after the dentary-squamosal joint was formed, the angular and articular rapidly degenerated and ceased to move with the jaw. The tympanic membrane, which possibly in the Cynodonts lay behind the plane of the articulation, probably in the early mammals became shifted more forwards and inwards, and the articular came to support the membrane by the development of the manubrium, while the angular also took part in the support of the membrane and became the tympanic bone. Gaupp is probably correct in regarding the goniale as not the homologue of the angular, but a distinct membrane-bone closely associated with the articular.

In the series of six diagrams given (text-fig. 53, A–F), the probable course of the evolution of the auditory ossicles is shown from the Cynodont type to the type found in the mammal. Though the first figure (A) represents the Anomodont type, this must not be looked upon as on the direct mammalian line, but as a specialised modification of the ancestral type. In fig. B we have represented the Cynodont type as seen in *Cynognathus.* The articulation is formed by the articular hinging on the quadrate and squamosal. The dentary almost reaches the joint. Fig. C represents the probable condition in the later Cynodont type when the dentary came to take part in the articulation. Fig. D represents the later stage when the quadrate has completely slipped out from the joint and the articular and angular have degenerated and no longer move with the dentary. In fig. E we have represented what was the probable condition when the articular and angular first became specialised for their auditory function. This is almost the Monotreme condition. Fig. F represents the condition in the typical higher mammal.

EXPLANATION OF PLATE LVI.

A.S.C. Ascending semicircular canal; *B.O.* Basioccipital; *B.S.* Basisphenoid; *Car.* Carotid artery; *E.O.* Exoccipital; *E.Pt.* Epipterygoid?; *F.O.* Fenestra ovalis; *F.M.* Foramen magnum; *H.S.C.* Horizontal semicircular canal; *Ju.* Jugal; *O.C.* Occipital condyle; *P.S.C.* Posterior semicircular canal; *Pt.* Pterygoid; *Q.J.* Quadrato-jugal; *Qu.* Quadrate; *Sq.* Squamosal; *St.* Stapes; *Ty.M.* Tympanic membrane; *Vest.* Vestibule.

Fig. 1. Left side of decalcified brain region of small Dicynodont. Nat. size.
2. Right side of partly decalcified brain-region of small Dicynodont. Nat. size.
3. Cast of osseous labyrinth of small Dicynodont, restored from the facts revealed by the two sides. Nat. size.
4. Quadrate region of *Oudenodon kolbei.* Reduced about one half. Front view.
5. Quadrate region of *Oudenodon kolbei.* Reduced about one half. Lower view.
6. Quadrate region of *Oudenodon kolbei.* Reduced about one half. Back view.